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NOTES ON NORTH AMERICAN SPHAGNUM, II

A. LEROY ANDREWS, PH. D.

THE SUBGENUS INOPHLOEA RUSSOW

Members of this group can readily be recognized as such in the field; if the large size and general aspect of the plants leave any doubt, it may readily be dispelled by examination under a hand-lens, as the cucullate leaf apices are unmistakable. Its species themselves are on the other hand most difficult to distinguish from each other without microscopical investigation, and show even then very close relationship. Long acquaintance in the field may lead one to suspect the specific identity of a newly found tuft of plants, or in some cases to be certain of it, but the group remains the hardest of all to collect with discrimination.

The stem leaves of all species of this group show the membrane of the hyaline cells almost completely or very largely resorbed on the outer surface. This matter of membrane resorption, studied most thoroughly by Russow, is to my mind one whose importance has not been adequately recognized in the systematic treatment of the genus. It occurs especially in the stem leaves, in some species also in the perichaetial leaves, sometimes on the one surface, sometimes on the other, sometimes on both. For its observation the leaf may be stained, but with good light and no condenser staining is superfluous. The membrane appears lacking in large gaps of more or less irregular form, but never with ragged outline, leaving often but a narrow border of membrane along the outer edge of the hyaline cell like a coating of ice about the edge of a pool; sometimes this is restricted to the two ends of the cell, or it may be so completely resorbed that no perceptible trace remains, in which last case one may easily fail to notice the lack of membrane. One's observation of the surface should be tested by transverse section, which leaves the condition unmistakable. A number of thin sections of the stem are sure to give some sections of stem leaves that can be used.

With reference to the structure of the perichaetial leaves already referred to, the statement of Warnstorf's descriptions that the basal and central portion is composed exclusively of chlorophyll cells is misleading in that one is likely to interpret it as referring to cells quite of the nature of the chlorophyll cells of the normal leaf structure, which is far from being the case. A transverse section of these

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perichaetial leaves is very instructive, as, if taken from the middle or basal portion of the leaf, it shows toward either end the normal alternation of large empty cells and small chlorophyll ones; after a shorter or longer distance, according to the species and the proximity of the section to the base of leaf, the chlorophyll cells become much enlarged, the others relatively smaller, until all are uniform. These uniform cells have their common walls pitted, they may contain as Russow noted, scattered chlorophyll grains, but appear otherwise empty, at least in case of plants with mature capsules; in fact a section of the dry perichaetial leaves shows them almost entirely collapsed; if water be applied to such a section under the microscope, the walls can be seen to immediately spring apart (this test may also be applied to leaves lying flat on the slide) and present then in hexagonal outline with outer walls projecting angularly, an accordion effect, which on sufficient soaking goes over, at least in part, to a series of nearly rectangular cells. The transverse contractibility of the perichaetial leaves is greatly increased by this cellular structure, in which fact its physiological function is perhaps to be sought.

The antheridial leaves of this subgenus present very little, if any, difference from normal branch leaves, and antheridia are not easy to find in herbarium material. Observations upon the organs of fructification of *Sphagnum*, preferably from the field and from fresh specimens, are much needed; so far as observed all species of this subgenus are always dioicous.

The subgenus is cosmopolitan in its distribution; only to the northward it probably does not extend quite as far as *Litophloea*: at any rate it is not yet known from Greenland or Spitzbergen.⁽¹⁾

1. *Sphagnum portoricense* Hampe, 1852. Warnstorf once expended a whole article upon the proof that this species was not distinct from *S. imbricatum* Hornsch.⁽²⁾ only to reverse his decision the year after, his attention in the meantime having been called by Schliephacke to the walls of the cortical cells of the branches.⁽³⁾ But this character had already been mentioned in a number of works and very clearly figured in no less than three.⁽⁴⁾ I allude to the fact because of its interest in connection with the history of the species, also because it illustrates two weaknesses of Warnstorf which we shall find frequently leading him into error: 1. an insufficient consideration of the work of other botanists, 2. unreliability in observations involving minute microscop-

(1) Cf. C. Jensen, *Musci Asiae borealis* III. 5. 1909.

(2) Hedwigia. 28: 303-8. *pl. VIII and IX*. 1889.

(3) L. c. 29: 67, *f.* 1890.

(4) Sullivant, *Icon. Musc.* 3, *f. pl. 2*. 1864; Braithwaite, *Month. Microsc. Jour.* 14: 47, *f.*, *pl. CX*. 1875. *Sphagnaceae of Europe and North America*, 32, *f.*, *pl. II*. 1880.

cal detail. Warnstorf's article is in spite of the oversight by no means without interest and value, and the close relationship of *S. portoricense* and *S. imbricatum* is indubitable, as had in fact been recognized before.

Both species are best separable from others of the group by the fact that their branch leaves in transverse section show the chlorophyll cells about equilaterally triangular with base of triangle exposed on inner surface of leaf and that the inner walls of their hyaline cells where in contact with these are normally beset by so-called fringe-fibrils, a series of close, nearly parallel, somewhat irregularly running ridges.

S. portoricense is distinguished from its parent species (for this is certainly the relation between the two) by its usually greater size, the more distinct hyaline border of its stem and branch leaves, by its strong horizontally spreading branches whose leaves increase gradually from the base, giving the branches a clavate effect, by the important difference in cortical cells of branches, and finally by the fact that its lower branch leaves are very short, in some cases wider than long, and all are more or less distinctly cordate at base, particularly, however, the lower ones.

The leaf border in *Inophloea*, best represented in the stem and lower branch leaves of this species, is something entirely different from the border of *Litophloea* in that it is a border of resorption. If examined closely in section and from both sides of the surface, it will be found to consist of a single plate of hyaline membrane with a fine mesh of darker lines, suggesting the remains of obsolete chlorophyll cells, though the mesh is much finer and must play a part in maintaining the rigidity of this rather broad but thin margin. This marginal membrane is a continuation of the inner leaf surface (the outer being here completely resorbed away), its outer edge is very irregular in outline, as is well illustrated in Warnstorf's figures in the article alluded to.

As to the cortical cells of branches, it may be noted generally that all species of *Sphagnum* show at base of branches a cortex resembling that of the stem, except that its cells do not constitute so many layers; usually the differentiated branch cortex shows its most characteristic development at about the middle of the branch, where the branch leaves are also best developed. In the case of *S. portoricense* the strong branches show a cortex most distinct well toward or quite at the apex, where the branch leaves are also largest and most characteristic, i. e. most differentiated from the stem leaves. The first noticeable peculiarity of these cells in *S. portoricense*, apart from their much greater size, is the fact that their outer walls do not show the pores usually present in other species of *Inophloea*, a fact noted already by Sullivant; secondly, the dividing wall between each

of these cells and that next below it in vertical series is not a plane one, but projects saccately, or in extreme cases in funnel form into the cell next below, providing connection with it by a pore at the end of the funnel.

These characters seem to distinguish the form amply from its parent species, *S. imbricatum*, but it is not inconceivable that further study of it in the field may reveal more nearly intergrading forms. Its range falls essentially within that of *S. imbricatum* and that in a characteristic region, which has more than all others in orth America evolved secondary forms from species of more general distribution in the northern hemisphere. I have seen specimens of it from New Jersey, Georgia, Florida and the West Indian island of Guadeloupe, which with the original Portorican station represent its present known range. It is in New Jersey aquatic in its preferences, being found according to Austin in shallow ponds. Further observations and collections are very desirable, as its reproductive organs and fruit are entirely unknown.

2. *Sphagnum imbricatum* Hornschuch, 1865. Russow's publication of Hornschuch's herbarium name of this species ⁽¹⁾ is generally regarded as adequate, though it contains no full description, hardly more in fact than mention of a single characteristic feature, but that of such a sort that there is no mistaking the plant's specific identity. Under the previous species we have already characterized it in the main; where the fringe-fibrils are present they are a sufficient diagnostic character, except in so far as it might be confused with *S. portoricense*; it must be noted, however, that they are not necessarily present throughout the leaf, but may be lacking in a greater or less portion from the apex downward, in some specimens occurring only in a few cells of the middle basal part and in the variety lacking entirely. There is in this feature constancy only in that in a given tuft of plants one finds the branch leaves of the various plants very closely similar, but in a number of collections all degrees may be represented, so that a division at any point becomes an arbitrary one.

An interesting character of this species was observed by Russow ⁽²⁾, but his description of it seems to me not altogether accurate. It has to do with the fibrils in the cortical cells of stem and branches. If one examine the inner walls of these cells where they are in contact with the wood cylinder, one finds a very notable and, so far as I have observed, entirely constant difference in that *S. imbricatum* (with *S. portoricense*) shows here not the normal continuation of the fibril-bands of the rest

(1) Russow, Beitrage zur Kenntnis der Torfmoose, 21. Dorpat, 1865.

(2) Zur Kenntnis der Subsecundum und Cymbifoliumgruppe der Torfmoose, 74, 93, 95. 1894.

of the inner wall, but a corrugated surface with alternate parallel ridges and grooves, the ridges continuing the spiral direction of the fibrils, being lower and less sharp in section though very much closer than the fibrils which they supplant. Russow did not differentiate these corrugations, except as to number, from the fibrils. A branch stripped of its leaves is easily examined with reference to this point, as it is generally possible to focus through the cortical cells without further cutting.

The type specimen of the species was from Kamchatka. For its North American distribution it is for the most part a coastal plant, ranging on the east coast from Newfoundland southward to Georgia, Alabama and Mississippi, and represented in a single collection from Cuba, being found once as far inland as Indiana. On the West its distribution is high northern, a couple stations on Alaskan islands forming with two Kamchatkan ones, one in East Siberia and a new one in Japan (Aramaki, Rikuzen, 27-5-1909, leg. Nematsu, comm. Iishiba) a somewhat isolated area, connecting neither through Asia nor North America with the European-eastern-North-American field of more general distribution. Another isolated area is represented at present by a single recorded station, the island of Chiloe off the coast of southern Chili.⁽¹⁾ This last almost startling fact of specific distribution is matched by that of several other species of *Sphagnum* as we shall see.⁽²⁾ Its European distribution agrees in general with its eastern North American, in that it is mostly coastal, though reaching as far inland as the mountains of Styria in Austria, and that it does not reach a very high northern latitude nor a high altitude. Most instructive as to its European habitat is the information and map furnished by K. F. Dusén with reference to its Scandinavian provenience.⁽³⁾ The northern limit set by him for its distribution on the western coast of Norway was somewhat confirmed by the experience of Kaalaas and the author, who failed to find it in extensive collections made along the coast of Söndmøre in the summer of 1907, though Kaalaas reports collecting it once previously in Orstenvik a trifle further north than Dusén's limit.⁽⁴⁾

The species may be sought anywhere along our eastern coast in usually compact masses of not over robust plants, often tinged brown-

(1) Cf. Braithwaite, *Sphagnaceae of Europe and North America*, 35. 1880.

(2) Braithwaite's statement of the collection of fertile (fruiting?) specimens of this species by Capt. King in Chiloe may rest upon a wrong identification. At any rate a specimen (fruiting) from the Mitten collection now in the herbarium of the N. Y. Botanical Garden labelled "*S. cymbifolium*, Chiloe, Capt'n. King" is *S. magellanicum*, the characteristic species of *Inophloea* in that region.

(3) Om *Sphagnaceernas* Utbredning i Skandinavien, 52, ff. 103, 121 f. Upsala, 1887.

(4) Bryophyten in Romsdals Amt. (Norske Videnskabers Selskabs Skrifter, No. 7 1910) 42. 1911.

ish, not infrequently associated with *S. palustre*, from which it is not easily distinguished without microscopical examination.

Var. *affine* (R. & C.) Warnstorf, 1889. This aspect of our species, first proposed as an independent species (*S. affine*) and well characterized by Renaud and Cardot⁽¹⁾, was correctly interpreted by Warnstorf. It differs from typical plants only in the complete lack of fringe-fibrils on inner walls of its hyaline leaf cells, in which character, as already noted, all degrees of transition are found. Its retention as a variety is desirable for practical reasons, as calling attention to this direction of variation and preventing confusion of this with the following species, *S. palustre*. From that species our variety is distinct by several characters, any one of which may in occasional specimens be found somewhat less strongly marked than normal. Most reliable is the leaf section which in *S. imbricatum*, as already noted, shows chlorophyll cells equilaterally triangular with hyaline cells very strongly convex on the dorsal surface, while *S. palustre* has chlorophyll cells isosceles triangular with short base and hyaline cells much less strongly convex on dorsal surface. The hyaline cells of the branch leaves of *S. imbricatum* show a membrane on the inner surface relatively more porose than that of *S. palustre* (at any rate in the case of the variety and the typical plants found within the variety's range), having large pores in a single row in each cell, even in those of the central part of the leaf, a condition foreign to *S. palustre*. This character of *S. imbricatum* is admirably shown by Roth's figure⁽²⁾ though he gives no corresponding figure of *S. palustre* with which to compare it. Similarly the outer membrane of the cortical cells of the stem of *S. imbricatum* is relatively more porose: in this species I have counted up to 10 pores per cell. The stem leaves of *S. imbricatum* are very constant in smaller size than in *S. palustre*, in a more spatulate or nearly quadrangular and less oval form, more distinct hyaline margin and complete lack of fibril bands in hyaline cells, points again well illustrated by Roth's figures.⁽³⁾ In the perichaetial leaves the border region of normal alternating cells is relatively narrower in *S. imbricatum*. Relying primarily upon the leaf section, but taking into consideration at the same time the other points mentioned one should have no trouble in separating *S. imbricatum* var. *affine* from the next related *S. palustre*.

In spite of Warnstorf's correct identification of this variety, it is questionable whether he fully understood it, as his *S. degenerans*⁽⁴⁾ and

(1) Rev. bryol. **12**: 44. 1885.

(2) Die europaischen Torfmoose, pl. I, fig. 2d. 1906.

(3) L. c., fig. 2a; cf. 1a.

(4) Bot. Centralbl. **42**: 102. 1890.

S. turfaceum⁽¹⁾ reduced by Russow⁽²⁾ and Limpricht⁽³⁾ to *S. palustre* he still insists⁽⁴⁾ are *S. imbricatum* var. *affine*. I can express no independent opinion upon the European forms in question, though I have little doubt from the literature mentioned that Russow and Limpricht are right; however, I can state very definitely that North American specimens from the Pacific coast region ascribed by Warnstorf to *S. turfaceum* and later with the withdrawal of that species, labelled *S. imbricatum* var. *affine* are *S. palustre*, the variety of *S. imbricatum* being entirely unknown from our Pacific coast, in fact from the whole region of distribution of *S. imbricatum* except Europe and eastern North America. Within this range it seems to be infrequent in Europe and in eastern North America hardly reaches as far south as the typical form. Along the New England coast it is abundant; it has been found as far from the coast as West Virginia.

3. *Sphagnum palustre* Linné 1753. Though it may seem strange to bryologists to see the familiar *S. cymbifolium* displaced by this older Linnean name, the restoration goes back to Lindberg, who studied the Dillenian herbarium and recognized the identity of the specimen in question.⁽⁵⁾ The species is in its typical form easily determinable, but its delimitation in either direction difficult. Its branch leaves show in section chlorophyll cells isosceles triangular with narrow base, straight or outwardly curving legs, thin walls, triangular to somewhat ovate-triangular lumen. The plant thus characterized is the most common of the subgenus in the northern hemisphere, where it is very generally distributed; though it has been regarded as cosmopolitan, its occurrence in the southern hemisphere is much in need of further investigation; in the case of South American specimens I have seen none that seemed clearly referable to this species, nor does Warnstorf accredit it to Central or South America.⁽⁶⁾ In North America it is common from Newfoundland southward to the Gulf states (Florida to Texas), from California to Alaska and far inland. This occurrence well throughout the north temperate zone seems to correspond with its distribution in Europe and Asia.

Under somewhat abnormal conditions the chlorophyll cells may be relatively more strongly developed, becoming wider and more or less trapezoidal in section, with bases exposed on both surfaces of

(1) Schriften der Naturf. Ges. Danzig, N. F., IX Bd., 2 Hft. 1896; I have not seen this description.

(2) Zur Kenntnis der Subsecundum und Cymbifoliumgruppe europäischer Torfmoose, 90. 1894.

(3) Rabenhorst, Kryptogamenflora 4³: 605. 1901.

(4) Kryptogamenflora der Mark Brandenburg 1: 325. 1903.

(5) Europas och Nord Amerikas Hvitmossor, 21. 1882; Kritisk Granskning af Mossorna uti Dillenii Historia Muscorum, 13. 1883; cf. also Druce and Vines, The Dillenian Herbarium, 202. 1907.

(6) Hedwigia 33: 336. 1894.

leaf, a fact apparently explaining the origin of the synonyms *S. degenerans* Warnst. and *S. turfaceum* Warnst. already mentioned. It should be said at the same time that specimens of *S. palustre* from our Pacific coast tend to have chlorophyll cells with a broad base, possible of confusion with *S. imbricatum* var. *affine* if one examine with reference to this character alone and that without sectioning the leaf. Both the section and the other characters place them with *S. palustre*. If the branch leaves of these Pacific coast specimens are examined on the inner surface the areolation is peculiar in that the chlorophyll cells, while very wide in their central part, are narrow at their ends, quite corresponding with Warnstorf's figure⁽¹⁾ of *S. pseudocymbifolium* C. M. from the Himalayas of Asia. That this last is specifically distinct from *S. palustre* is, however, questionable in the extreme.

Anyone collecting *Sphagna* in the United States or British America is sure to get *S. palustre* and will want directions for avoiding it rather than the contrary. I can, however, give none. So far as distinction is possible in the field one should learn to distinguish the others of the subgenus and assume that all specimens not strongly characteristic belong to *S. palustre* unless one is collecting in a locality of special interest or is otherwise enabled to collect everything. Its colors are green to brown, it generally grows compactly, may be robust, and fruits rather frequently.

4. *Sphagnum henryense* Warnstorf 1900. This species was discovered by Kearney in the region of Cape Henry, Virginia, from which place it takes its name.⁽²⁾ Its specific value was recognized and well diagnosed by Warnstorf⁽³⁾. The chlorophyll cells of its branch leaves have in section the shape and position of those of *S. palustre*, nor is there much in its external appearance to separate it from that plant. Its chief peculiarity is the condition of the inner walls of the hyaline leaf cells where they overlie the chlorophyll cells, their surface being roughened by a very fine-meshed network of prominent ridges, especially in the lower part of leaf. The fact that this surface is roughened will be noted on microscopic examination of inner leaf surface, also of transverse section of branch leaf, but its exact nature can only be made out, as Warnstorf emphasizes, by longitudinal leaf sections, best secured by sectioning longitudinally one of the short branches of the capitulum. It will then be found to be entirely different from the papillae of *S. papillosum* and more closely resembling the condition of *S. imbricatum*, differing, however, in the fact that the ridges are not nearly so high, so that they do not give the fringe-fibril effect of that species, and that they form a network

(1) Hedwigia 30: pl. xx, fig. g. 1891.

(2) Cf. Contributions U. S. Natl. Herb. 5: no. 6, 510. 1901.

(3) Hedwigia 39: 107. 1900.

with very fine mesh, while those of *S. imbricatum*, though somewhat irregular and often curving in direction, tend to run parallel with rather than cross each other, only occasionally forking. The species shows no other characters suggesting relationship with *S. imbricatum*, but is obviously more closely related to *S. palustre*; the numerous, clearly defined, nearly round pores on the outer surface of the branch-leaves give a distinctive appearance noted also by Warnstorf in the original description. The recognition of this species is one of Warnstorf's most valuable contributions to North American sphagnology. This in spite of the fact that he seems to have forgotten it for a time, for specimens of it collected by Mr. H. H. Bartlett in Georgia received from Warnstorf the herbarium-name *S. Bartlettii*, only to be reduced by him later, according to a letter from Mr. Bartlett, to *S. henryense* as its variety *Bartlettii*. They correspond entirely with his description of the species and form the basis of my knowledge of it, as I have not seen the type. According to Mr. W. R. Maxon, through whose kindness I was enabled to see the types of the species proposed by Warnstorf from Kearney's Dismal Swamp collections, there is no specimen of *S. henryense* in the U. S. National Herbarium, so it is evidently accessible only in Warnstorf's herbarium, now the property of the Berlin Botanical Museum. Other specimens entirely identical collected by Bartlett in the same locality as his *S. Bartlettii* (Branch Swamp, McDuffie Co., Ga.) were wrongly named by Warnstorf, *S. subbicolor* Hampe.

In 1907⁽¹⁾ Warnstorf described *S. alegrense* from Brazil, characterized by the same condition of the cell walls, erroneously stating it to be his first observation of this character in the genus; whether it is really distinct from *S. henryense* I should not undertake to say from the description, though the chlorophyll cells are described as of somewhat different section.

In looking through the material of the New York Botanical Garden, I find one other specimen of our species from Delaware (Laurel, collected by Commons, 1893, No. 65), which leaves its present known distribution Delaware, Virginia, Georgia. It is then one of the species characteristic of our southern Atlantic coast, as for example *S. portoricense*, and may be looked for from New Jersey to Florida. Its organs of fructification as well as its fruit are as yet unknown.

Ithaca, N. Y.

(1) Hedwigia 47: 83, f.